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# A REVISION OF THE AUSTRALIAN ANT GENUS *NOTONCUS* EMERY, WITH NOTES ON THE OTHER GENERA OF MELOPHORINI

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## No. 6—*A Revision of the Australian Ant Genus* NOTONCUS *Emery, with Notes on the other Genera of Melophorini*

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At the present time, *Notoncus* must still be listed among those formicine genera that are easy to recognize by habitus, but that cannot be adequately characterized in the formal sense. Fully limiting diagnosis will not be possible in these cases until the tribes and genera of the world Formicinae have been thoroughly examined and revised; the classifications of the subfamily and the tribes now in general use (Wheeler, 1922, 1935; Emery, 1925) are artificial and based on serious misconceptions. My colleagues, E. O. Wilson and T. Eisner, are now engaged in different phases of the work necessary to provide a skeleton revision of the tribes and genera of the Formicinae, but owing to the size and complexity of the task, final results will not be ready for several years.

The work already done by Wilson and Eisner, and a certain amount completed also by myself, has yielded a great deal of information on the phyletic distribution of important characters, such as proventricular structure and function, form and placement of propodeal spiracles, mandibular dentition in all castes, wing venation, male genitalia, and so on. While the work is not yet far enough advanced for us to predict what a natural tribal arrangement will look like, it will be sufficient to say that a new arrangement will differ considerably from those available. Insofar as the limits of tribe Melophorini are concerned, the same probably holds true, but for the purposes of this paper, we can continue to treat as melophorines the same genera listed in the most recent classification of the tribe (Wheeler, 1935). These genera have in common a "short" type of proventriculus (as contrasted with the "long" type of Formicini and Camponotini), and they are distributed in an "Antarctic" pattern more or less paralleling that of the unrelated ant groups *Heteroponera* Mayr and *Monomorium* (*Notomyrmex*) Emery. These characteristics do not, however, separate the Melophorini from other short-proventriculate groups that are well represented in the Southern Hemisphere (e.g., *Myrmelachista, Stigmacros*).

Wheeler's 1935 classification, while perhaps the best so far offered for the tribe, is so excessively synoptic that it is little more than a list of genera and subgenera, with type citations and a listing of the then included species. Wheeler avoided the diffi-

culty of characterizing the genera simply by omitting any reference to particular, concrete characters. The insight that afforded his classification a certain logic as compared to older systems was apparently a result of his second trip to Australia (1930-1931), and was derived at least in part from or in discussion with Clark (Clark, 1934). Neither Wheeler nor Clark ever attempted to place this system on a solid morphological basis. Here is Wheeler's 1935 generic arrangement of the Melophorini:

*Myrmecorhynchus* Emery
*Lasiophanes* Emery
*Prolasius* Emery
*Pseudonotoncus* Clark
*Melophorus* Lubbock
  subgenus *Melophorus s. str.*
  subgenus *Erimelophorus* Wheeler
  subgenus *Trichomelophorus* Wheeler
*Notoncus* Emery
*Diodontolepis* Wheeler

As already suggested, it is premature to consider that all of these groups really belong to a single tribe. If any genera were to be separated now, *Myrmecorhynchus* might be the most likely candidate for exclusion, as indeed it has been excluded in the past. Such questions are passed over here. *Myrmecorhynchus* is a genus inhabiting southeastern Australia, where it ranges from southeastern Queensland (Clark, 1934) to the western end of Kangaroo Island, South Australia (personal collection, unreported). It tends to be arboreal in foraging habits, and apparently some of the species normally nest in arboreal situations. With some patience, an investigator of these little-known ants should be able to trace individual workers to the nest by offering them honey baits. The specific identity of the genotype is uncertain, and may have been confused by Wheeler (1917). In 1934, Clark added descriptions of three species. I have found it impossible to determine specimens in my possession from the existing literature. This genus requires much closer study than it has had up to now.

*Lasiophanes*, the only neogaeic melophorine genus, is restricted to southern South America. The Argentinian species have been revised by Kusnezov (1951), who drastically reduced the number

of names by extensive synonymy. While this is not the final word on the species-level taxonomy of *Lasiophanes,* it is certainly a vast improvement over previous arrangements. *Lasiophanes* is supposed to differ constantly from other melophorines by the presence in the wings of the sexes of the medio-cubital crossvein (m-cu), which closes the discoidal cell, and by the confluence of the clypeal and antennal fossae. Present indications are that the genus contains not more than half a dozen closely related and rather variable species.

The Australian-New Zealand group *Prolasius* was raised by Clark and by Wheeler to generic rank distinct from *Melophorus,* an action that can now be supported by the discovery of good characters for separating these two genera (see below). Wheeler placed *Notoncus hickmani* Clark and *N. rotundiceps* Clark in the genus *Prolasius,* but it will be shown later in this paper that these really belong in *Notoncus.* The placement of *Melophorus scipio* Forel remains uncertain.

The species of *Prolasius* are medium-small to small in size, and black, brown, reddish or dull yellow in color. They resemble in habitus and to some extent in habits certain Holarctic species of *Lasius, Prenolepis* and some of the *Formica neogagates* group of North America, but they are generally more restricted ecologically than are their northern analogues, taken species for species. The nesting sites are restricted to those parts of Australia, including Tasmania, and New Zealand having a cool or temperate climate and good rainfall, and which therefore support a good forest cover. The workers show little or no polymorphism, their propodeal spiracles are small and round, and the mentum is without ammochaetae. Sculpture is reduced and fine, or smooth, and standing pilosity is usually sparse. Species taxonomy is reviewed in a paper by McAreavey (1947).

*Pseudonotoncus* Clark was based on the single species *Ps. hirsutus* Clark, from the Otway Peninsula of western Victoria. It is, however, widespread also in the vicinity of Melbourne, where I found it in medium-rainfall sclerophyll forest at Research and at Arthur's Seat above McCrae. The nests I saw were built in the soil without covering objects or detectable craters, and workers as well as frequent dealate females were found foraging over shrubs for nectar and honeydew. Donisthorpe (1937) described a color form, *Ps. turneri,* from Tamborine Mt., Queens-

land, but this is probably not specifically distinct from *hirsutus*. *Pseudonotoncus* is distinct from other melophorine genera in habitus and in possessing long, acute, paired propodeal and petiolar teeth.

## MELOPHORUS Lubbock

*Melophorus* Lubbock, 1883, Jour. Linn. Soc. London, Zool., 17: 51. Genotype: *Melophorus bagoti* Lubbock, 1883, monobasic.

< *Melophorus* (*Melophorus*), Emery, 1925, Genera Insect., 183: 11 (see for further synonymy).

> *Melophorus* (*Melophorus*) Wheeler, 1935, Psyche, 42: 71.

> *Melophorus* (*Erimelophorus*) Wheeler, 1935, *loc. cit.* Subgenotype: *Melophorus wheeleri* Forel, 1910, by original designation. New synonymy.

> *Melophorus* (*Trichomelophorus*) Wheeler, 1935, *loc. cit.* Subgenotype: *Melophorus hirsutus* Forel, 1902, by original designation. New synonymy.

After separating *Prolasius* and *Diodontolepis* from *Melophorus*, Wheeler divided the remaining Australian species into the three subgenera listed in the synonymy above. This division was said to have been made on the basis "mainly of thoracic structure," but Wheeler never revealed exactly what characters he had in mind. As already mentioned, concrete differential characters among the melophorine genera were ignored in Wheeler's 1935 classification; in their place, he substituted vague statements such as that *Melophorus* was "Cataglyphis-like," *Erimelophorus* "Pheidole-like," *Prolasius* "Lasius-like," and so forth. This looseness apparently misled McAreavey (1947), who found Wheeler's division of *Melophorus* "a useful one," and then proceeded to develop Wheeler's words "Pheidole-like" into "others harvest grain," but without citing the slightest bit of evidence for a habit which, in a formicine ant, would surely call for some documentation.

My own extensive observations on diverse *Melophorus* species referable to all three of Wheeler's subgenera, as found in desert, coastal dune and woodland habitats in many parts of Australia, do not include a single instance where any of the ants were found carrying seeds. On the contrary, all species were found to be fast-running predators of the *Myrmecocystus* and *Cataglyphis* class, so characteristic of arid Northern Hemisphere sections. As is well known, some of the species of *Melophorus* are "honey-

ants," with repletes analogous to those of *Myrmecocystus* spp. In my opinion, such lightning-quick predatory habits and honey- or nectar-feeding are complementary adaptations for xeric environments best developed in the Formicinae. In all of the same xeric localities in Australia (as well as in other parts of the world), one also finds myrmicine genera that are the true specialized harvesters; as a general rule these myrmicines forage, whether in search of seeds alone or of their usual mixed animal-vegetable diet, at a considerably more sedate pace.

The "harvesting" of seeds by formicines is not unknown, but the circumstances of such activities usually point to myrmecochoric adaptations of the seeds or to relationships other than the utilization of the entire seed contents as food by the ants. Myrmicines, on the other hand, can apparently draw nourishment from the entire contents of the seed that will sustain them over considerable periods of time. This is not true of many genera of myrmicines with predominantly insectivorous or otherwise specialized food habits, of course, and even the specialized harvesters among the myrmicines may require some animal protein for the survival of the nest economy. It should not be assumed that the presence of a polymorphic worker series including large-headed majors is evidence of harvester specialization like that of many *Pheidole* species, for such assumptions lead to obvious absurdities when the diversity of types of polymorphism among ants is considered (cf. Wilson, 1953). The seed-gathering activities of ants are treated by Bequaert (1922) and by Stäger (1929), both of whom cite further references.

My good friend Mr. John Mitchell, of the South Australian Museum, has called my attention to a note (Mitchell, 1948) on the environment of the agamid lizard *Tympanocryptis maculosa* Mitchell. This lizard was found on the salt-encrusted, four-mile-wide "marginal area" of the then long-dry Lake Eyre, in the desert of northern South Australia. Mitchell states that, "In this barren habitat one immediately wonders as to the food of these lizards. An examination of the stomach contents has revealed it to consist mainly of small harvest ants (*Melophorus* sp.) which apparently feed on the numerous seeds which are blown out over the lake, or alternatively, as was suggested by Madigan (1930), on micro-organisms in the salt." On my query, however, I learned from Mitchell that the determination of the ants, and

their denomination as "harvest ants," were furnished by none other than Father McAreavey! It seems to me likely that Madigan's opinion has the better chance of being correct, and I may mention also that I have observed on other dry Australian salt lake-beds that not only seeds, but also winged insects in large numbers, are blown far out onto the uninhabitable crust. In addition, a few kinds of insects appear to be at home on the salt crust.

No matter what harvesting propensities or lack of them among *Melophorus* species may eventually be demonstrated, I still fail to find any fundamental differences between the species Wheeler assigns to *Melophorus s. str.* and those he puts in *Erimelophorus*. Both "groups" produce large-headed soldier forms, and interspecific variation in alitruncal structure runs without any particular regard for his suggested division. The subgenus *Trichomelophorus* is based on an admittedly aberrant species, *M. hirsutus* Forel, but even here the alitrunk is not so markedly different in basic structure as to suggest a split on this character alone. The subgeneric name suggests that Wheeler was unduly impressed by the striking long and abundant pilosity, but if so, then he did not take into proper account the fact that another undetermined *Melophorus* in his own collection combines very similar pilosity with a more nearly "typical" *Melophorus* alitrunk. In short, I am unable to support Wheeler's subgenera on either morphological or ethological grounds.

On the other hand, I have now seen a majority of the Australian Melophorini species, and I am impressed by a set of characters that will, I believe for the first time, permit objective diagnosis of *Melophorus* (*s. lat.*) as a distinct genus. The following remarks refer only to the worker and female castes. Most *Melophorus* have elaborate and well-developed sets of ammochaetae on the gula, mentum, clypeus and mandibles. In a few small forms inhabiting more mesic areas, the ammochaetae may be much reduced. Nevertheless, if the extensive and varied sample I have seen is fully representative, the ammochaetae are never wholly lost in any true *Melophorus*. In all species I have seen, at least one or two pairs of sturdy, long, J-shaped hairs are to be found arising from the base of the mentum, their tips curving anteriorly under the mandibles. In exceedingly hairy forms, such as *M. hirsutus*, the mental ammochaetae may be difficult to see, and in

worn or damaged specimens they may occasionally be missing, but the coarse pits from which they arise can always be found under high enough magnification or by dissection.

Another character is easier to use, and this has been found perfectly correlated with the ammochaetal character in all species reviewed. This concerns the shape of the propodeal spiracles, which in *Melophorus* are narrow and elongate, in the form of a slit or comma.

In melophorines of all other genera, in all of the many species I have examined, ammochaetae are absent from the mentum, and the propodeal spiracles are round or broadly oval. *Melophorus* is usually rather highly polymorphic in the worker caste, but this character is difficult to utilize for practical identification, and it is not an absolute generic difference among the melophorines. Two possibly aberrant species I have never seen, and which are incompletely described: *M. fulvihirtus* Clark and *M. scipio* Forel, are placed in *Melophorus* with doubt.

In Australia, to which country *Melophorus* is apparently confined, the genus is commonest in arid regions, especially in the central and southern parts, and several species occur on both littoral and inland dune systems. A few small species occur in medium-rainfall forest types, but the wettest forest types appear to exclude them in favor of *Prolasius* and other genera. In general, *Melophorus* is impoverished in mesic environments, and the ammochaetae and narrowed propodeal spiracles, obvious adaptations to a xeric habitat, make it likely that the genus arose in response to the increasing availability of arid situations back in the geologic past of the continent. The ancestral stock may have been *Prolasius*.

## Notoncus Emery

*Notoncus* Emery, 1895, Ann. Soc. Ent. Belg., **39**: 352. Genotype: *Camponotus ectatommoides* Forel, 1892, monobasic.

> *Notoncus* Emery, 1925, Genera Insect., **183**: 14. Wheeler, 1935, Psyche, **42**: 71.

> *Diodontolepis* Wheeler, 1920, Psyche, **27**: 53. Genotype: *Melophorus spinisquamis* André, 1896, by original designation, monobasic. Clark, 1934, Mem. Nat. Mus. Victoria, Melbourne, **8**: 64. Wheeler, 1935, Psyche, **42**: 70. New synonymy.

< *Melophorus* (*Melophorus*), Emery, 1925, Genera Insect., **183**: 12.

Had we to deal here only with the species placed in *Notoncus* before 1930 (*ectatommoides, gilberti* and *enormis* in the sense of this paper), generic diagnosis would be simplicity itself, for the workers of these species all have the pronotal humeri and scutellum hypertrophied and unusually salient in one form or another. Unfortunately for this neat little arrangement, Clark described in 1930 two species, *N. hickmani* and *N. rotundiceps,* that are very like the "typical" *Notoncus,* but in which the hypertrophy of the alitruncal components is suppressed and ambiguous. Actually, Clark's two species appear to be large and small allometric variants of one species, *N. hickmani* (*q. v. infra*), but this does not affect the status of this species with respect to generic placement.

Wheeler (1935) shifted Clark's species into *Prolasius,* but McAreavey rejected this placement because he was misled by the original descriptions into thinking that the types, unlike *Prolasius* workers, were without ocelli. However, ocelli can be demonstrated in *hickmani* workers, particularly the larger ones, under good circumstances. The presence of ocelli does not make *hickmani* a *Prolasius,* for there exist differences of habitus that I believe most myrmecologists will accept until the proper study of *Prolasius* enables us to state satisfactory generic characters for that group. The current taxonomy of *Prolasius* (Clark, 1934; McAreavey, 1947) does not seem to me to reflect very accurately the species in collections I have seen.

The really significant relationships of *N. hickmani* appear to me to be with the three "typical" *Notoncus* species on one side, and with *Diodontolepis spinisquamis* (André) on the other; in fact, I regard *hickmani* as the perfect intermediate linking these superficially disparate types in one genus. The alternative to this merger would be the segregation of *hickmani* and *spinisquamis* in one genus (*Diodontolepis*) apart from the "typical" *Notoncus,* but in this case, the generic split would have to rest entirely, so far as known characters go, on the degree of hypertrophy of the elements of the alitrunk already mentioned. The larger workers of *hickmani* clearly show a tendency toward hypertrophy, however, and certain series of *N. enormis* (and perhaps other species) show such general damping of the usual hypertrophied elements that the specialist becomes aware that any dividing line drawn on this basis is ambiguous with respect

to at least some nest series. The development of the various elements of the alitrunk appears to respond in a correlated way to an overall genetical factor controlling the general degree of hypertrophy, and it is the instability and gradational nature of this factor that prevents us from using it as a generic character. Other points of similarity, at least in the female and worker castes examined, indicate close relationship of *spinisquamis* and *hickmani* to the other *Notoncus*, and their separation on the present evidence would be arbitrary and of little practical taxonomic value. Emery (1925) had retained *spinisquamis* in *Melophorus*, but in this he was mistaken (Clark, 1934; Wheeler, 1935). It can now be shown that all of the species here included in *Notoncus* lack the mental ammochaetae of *Melophorus* and possess round or nearly round propodeal spiracles.

The species of *Notoncus* are medium-small to medium in size, with color ranging from yellow to piceous. Internidal allometry is often marked, and *enormis* shows sufficient intranidal allometry over its usual size range that it deserves to be called "polymorphic"; however, even *enormis* cannot rival in this respect the more highly polymorphic species of *Melophorus*.

The species of *Notoncus* are, so far as known, confined to Australia, including Tasmania. All five of the species are found in eastern Australia, and two of them occur sporadically through the less extremely arid parts of South Australia, to reappear in southwestern Australia. The distributions of the species are summarized in greater detail below.

## A Summary of Species-Level Taxonomy in *Notoncus*

Unfortunately for later developments in species-level taxonomy of the genus, the workers Emery described and figured in 1895 as "*ectatommoides*" are not the corresponding caste of the original female type of Forel's *ectatommoides*. The females and workers of all the valid *Notoncus* species have now been properly associated, and it is reasonably clear from Forel's original *ectatommoides* description that he had a specimen agreeing with the characters as given for that species in the key to the females below. Emery's workers belong to the species described by Szabó as *enormis*, which is the first available name, and the one adopted here. The worker and female of *enormis* match in having the gastric dorsum densely pubescent, and they differ from the

respective castes of *ectatommoides* by the same character.

The species *capitatus* Forel and *capitatus* var. *minor* Viehmeyer are obvious synonyms of *enormis* described through a lack of appreciation of the polymorphism shown by this species. *N. mjöbergi* refers to the variant, sporadic in Queensland, in which the hypertrophy of the humeri and scutellum is relatively more or less feebly expressed; intergradient forms prevent our accepting it as a distinct species, and there is no clear evidence that it forms geographically distinct populations in eastern Queensland.

The species *ectatommoides*, previously resting on a single female labelled "New Zealand," was recognized by both Forel and Emery as an Australian endemic. The accompanying species with similarly erroneous locality labels were indicative of a South Australian provenience, and it is quite possible that *ectatommoides* was first taken in the vicinity of Adelaide. Donisthorpe's species *rodwayi*, also described from a female, does not seem to differ in any significant way from the *ectatommoides* type, and I feel confident that it is a synonym on the basis of descriptions and considerations of locality. The worker associated with the *ectatommoides* female (in the same nest series) agrees well with the description of *foreli* by André or with the descriptions of one of the *foreli* varieties described later. André cited the original locality of *foreli* as "Australie occidentale," but this may be in error. This species has not been reported since from Western Australia, despite considerable myrmecological exploration of that state; on the other hand, in the same paper wherein André described *foreli*, he described several other ant species from the "Alpes de Victoria." The *Notoncus* species in question is very common in the Victorian Alps, and there is little question from all the descriptions concerned that *foreli* and the varieties *dentata*, *subdentata* and *acuminata* are all representative of the highly variable species properly called *ectatommoides*.

*N. gilberti* Forel is a smooth form related to *enormis;* it has several named subspecies and varieties, all synonymized under the species heading below, and *politus* Viehmeyer seems from the description to be an obvious synonym.[1]

[1] The Australian ant species of Viehmeyer were mostly published posthumously, apparently in large part from incomplete notes. It is by no means certain that Viehmeyer himself would have gone through with the publication of all these forms as novelties had he lived long enough, for a large proportion in all subfamilies belongs in the obvious synonymy of well-known species. Such posthumous publications, arranged by well-meaning friends of the deceased as his last memorial, are more likely to end by ruining his reputation. The section of posthumous papers in the "Cho Teranishi Memorial Volume," published in Japan by Teranishi's friends in 1940, is a similarly unfortunate case.

*N. hickmani* (=*rotundiceps*) and *N. spinisquamis* are relatively uncomplicated cases taxonomically, completing the roster of the genus as known at present. A synoptic list of the species and synonyms is offered below as a clarifying summary of changes here proposed in the species-level taxonomy of *Notoncus*.

N. ectatommoides (Forel), 1892
=foreli André, 1896, n. syn.
= " var. dentata Forel, 1910, n. syn.
= " var. subdentata Forel, 1910, n. syn.
= " var. acuminata Viehmeyer, 1925, n. syn.
=rodwayi Donisthorpe, 1941, n. syn.
N. enormis Szabó, 1910
=ectatommoides *sensu* Emery, 1895, *nec* Forel.
=capitatus Forel, 1915, n. syn.
=mjöbergi Forel, 1915, n. syn.
=capitatus var. minor Viehmeyer, 1925, n. syn.
N. gilberti Forel, 1895.
= " var. gracilior Forel, 1907, n. syn.
=politus Viehmeyer, 1925, n. syn.
=gilberti annectens Wheeler, 1934, n. syn.
= " " var. manni Wheeler, 1934, n. syn.
N. hickmani Clark, 1930.
=rotundiceps Clark, 1930, n. syn.
N. spinisquamis (André), 1896, n. comb.

## A Summary of the Known Distribution of the Five Species

The full ranges of each of the species differ, but there is broad overlap. In any one circumscribed and ecologically uniform area, there are no known cases where more than two of the species occur together. The most abundant and successful species within its range, and also the most variable structurally, is *ectatommoides,* which is abundant in the more open, grassy areas from east-central Queensland south through southeastern Australia to the Flinders Ranges and the vicinity of Adelaide. The extremes of environment occupied are the cool, moist mountain forest of grassy-floored intermediate sclerophyll type, common in the Australian Alps, and the arid, semi-oasic pockets in and near the Flinders Ranges, such as that at Wilpena Pound. Trees of moderate to large size seem always to be within foraging dis-

tance of the nests. In mallee, open woodland and heath country in Victoria and South Australia, *hickmani* tends to replace *ectatommoides* in many areas.

In Western Australia, on the far side of the barren Nullarbor Plain and its flanking arid tracts, *hickmani* is found again in the Perth-Albany "corner," a section in which, as already discussed above, the true *ectatommoides* probably does not occur. The only other *Notoncus* species certainly known from southwestern Australia is *gilberti* Forel, which appears to be abundant in the Perth district, and which is closely sympatric with *hickmani* in at least some areas east to Norseman and Esperance.

*N. gilberti* is not found again until, coming eastward, one meets with a restricted colony in the Flinders Ranges of South Australia; in one locality here, *gilberti* was found nesting very obscurely in the most heavily shaded and moist habitat available, in an area very densely populated by *ectatommoides*. After the Flinders Ranges oases, *N. gilberti* is found sporadically through eastern New South Wales and Queensland, in most cases, apparently, within the range of *ectatommoides*, and often at the same exact localities as the latter. The head form of worker and female *gilberti* resemble those of certain parasitic ants, and it is not beyond possibility that *gilberti* founds its nests by parasitizing species like *ectatommoides* (in the eastern states) and *hickmani* (in southwestern Australia). It should be emphasized that such a relationship is at present purely speculative.

*N. spinisquamis* and *N. enormis* live in or on the margins of very wet forests in eastern Australia; *spinisquamis* appears to occupy the cooler wet sclerophyll forests of Victoria and Tasmania, while *enormis* exists in the more tropical forests of eastern New South Wales and Queensland, farther to the north; both species exclude from their domains the widespread *ectatommoides*, which accompanies them through most of their ranges in adjacent intermediate vegetation types, but does not enter the wettest forest when they occur there.

At present, our knowledge of the distribution of all of these species and of their ecological limitations, diurnation of foraging, etc., is only very fragmentary. For this reason, we cannot say with confidence whether the seeming geographical variation in "habitat preference" is correlated with the distributions of various potential competitors; but in stating my preliminary

hunch, I believe that this will be found to be the case when *Notoncus* is better known. From a combination of morphological and distributional evidence, we may be safer in designating *spinisquamis* and *hickmani* as primitive types within the genus; it seems likely that *gilberti*, *enormis* and *ectatommoides* arose from something like *hickmani*.

Our knowledge of the habits of *Notoncus* species is very limited. The general method of nest-founding is probably of the claustral type, usual among formicines (see account of nuptial flights below), with reliance on a single dealate female. The nests are made in the soil, usually without covering rocks or other objects; the galleries extend beneath rocks more frequently in mountainous localities with high rainfall. The nests are most often, perhaps always, built near trees or large shrubs; in the few cases in which I have observed them directly, the *Notoncus* appeared to be climbing the trees for sugar secreted by various homopterans, but these cases were not favorable for the direct determination of the methods used by the ants in securing the honeydew. On a few occasions, root coccids or aphids have been observed in groups in the galleries of *N. ectatommoides*. Foraging activities take place outside the nest and above-ground, and all the species appear to be nocturnal or crepuscular foragers in varying degrees; diurnation of foraging activities, however, is highly variable with the seasons and with differing habitats, and possibly also according to the potential competitors present.

The nests are rather populous, in my experience, though this may not be obvious from superficial excavations made during the daytime, when most of the ants are at lower levels in the nest. The nests may extend over considerable territory without showing noticeable outward signs of their presence except, perhaps, for very small, irregular piles of excavated soil scattered at intervals in such a way as to be nearly imperceptible to the casual searcher. The workers run fairly rapidly, and tend, especially during the daytime, to take advantage of whatever cover exists in the form of soil-surface litter or loose bark on tree trunks. When the nest is breached, the workers show little aggressiveness, and hide readily whenever possible; however, they do show persistence and efficiency in removing the brood to safety.

Records for the production and nuptial flight of the winged sexes show wide seasonal variation within and between species;

our data are still too scanty to show a general pattern. Probably the flight time is controlled by temperature-humidity factors that reach optima at different times in different parts of the continent.

G. C. and J. Wheeler (1953, pp. 130, 211, pl. 1, figs. 6-11) have described the larva of *N. ectatommoides* (=*N. foreli*) in their comparative study of formicine larvae. Possibly in part as a result of ideas I once expressed to them in a letter, the Wheelers speculatively suggest the possibility that the ectatommine ponerines may have given rise to the original *Notoncus* stock. I have since had the opportunity to study the adult morphology of both *Notoncus* and the Ectatommini in much greater detail, and in relation to a fairly satisfactory general scheme of ant phylogeny (Brown, 1954), with the result that I must now consider *Notoncus* and the ectatommines to have come from very different basic formicid stocks. Under this interpretation, such suggestive similarities as exist must be considered as due to convergence.

### *Key to the species of* NOTONCUS: *workers*

1. Scutellum hypertrophied, projecting dorsad as a rounded tumulus or ovoid process, or as an erect scale, furcula, or tooth, from the region between the mesonotum and propodeum; humeri strongly developed, angulate and salient ..... 2.
   Scutellum absent, or at best not sharply differentiated and not forming any kind of prominent process projecting dorsad (in some workers of *N. hickmani*, the metanotal spiracles may be connected by a cariniform vestige); humeri rounded, not projecting to any marked extent ..... 4.
2. Scutellum in the form of a slender, erect process, the apex of which may be in the form of a chisel point, an emarginate chisel point, a Y, a thick, pointed tooth, or some intermediate shape (s. Queensland to S. Australia, sporadic in dry inland areas) ..... *ectatommoides* (Forel)
   Scutellum in the form of a thick, rounded tumulus or ovoid process 3.
3. Alitrunk at most very finely and superficially sculptured, so that it can be described as smooth and shining; gastric dorsum with only extremely sparse punctulation and appressed pubescence; mandibles finely striate over most of dorsal surfaces. (N. S. Wales, e. Queensland, sw. Australia, sporadic in Flinders Ranges of S. Australia) ..... *gilberti* Forel
   Alitrunk distinctly, widely, and rather coarsely striate, and largely subopaque throughout; gastric dorsum densely punctulate and with dense appressed pubescence; mandibles largely smooth and shining above, with coarse punctures (moist subtropical and tropical forests of e. Queensland and N. S. Wales) ..... *enormis* Szabó

4. Large, slender species with long appendages, the antennal scapes much longer than (usually at least 1.2x) the length of the head proper, including clypeus (Victoria, Tasmania) ..... *spinisquamis* (André)
Smaller, more robust species, the antennal scapes rarely, if ever, longer than the head proper, including clypeus, and usually shorter (widespread in se., South and sw. Australia) .....*hickmani* Clark

### *Key to the species of* NOTONCUS: *females*

1. Antennal scapes much longer than head proper, including clypeus (ratio usually about 1.2: 1.0); large, usually yellowish form with long legs... ..... *spinisquamis* (André)
Antennal scapes usually shorter than, rarely about equal to, length of head proper, with clypeus ..... 2.
2. Normally exposed surfaces of gastric dorsum densely micropunctulate and with dense appressed pubescence ..... *enormis* Szabó
Gastric dorsum with at most very sparse and inconspicuous punctulation and pubescence ..... 3.
3. Dorsal surfaces of mandibles largely smooth and shining, with scattered coarse punctures; striation absent or limited to feeble peripheral remnants ..... *ectatommoides* (Forel)
Dorsal surfaces of mandibles finely striate over all or nearly all of their dorsal surfaces, in addition to the coarse punctation usually present here ..... 4.
4. Head in dorsal full-face view subrectangular, with nearly straight sides, rather abruptly rounded occipital angles, and transverse, feebly convex posterior border ..... *gilberti* Forel
Head in dorsal full-face view ovoid, with strongly convex sides and broadly rounded occipital angles ..... *hickmani* Clark

## SYSTEMATIC TREATMENT BY INDIVIDUAL SPECIES

### NOTONCUS ECTATOMMOIDES (Forel)

*Camponotus ectatommoides* Forel, 1892, Mitt. Schweiz. ent. Ges., 8: 333, female. Type locality: probably [South] Australia, though original label of genotype indicated New Zealand as locality. Holotype: apparently in Mus. Civ. Stor. Nat., Genova, Italy.

*Notoncus ectatommoides*, Emery, 1895, Ann. Soc. Ent. Belg., 39: 353, female, *neo* worker.

*Notoncus foreli* André, 1896, Rev. Ent., Caen, p. 256, worker. Type locality: "Australie occidentale," probably in error; see above in the summary of species-level taxonomy in *Notoncus*. The type probably came from the Australian Alps. Holotype: Mus. Hist. Nat., Paris. New synonymy.

*Notoncus foreli* var. *dentata* Forel, 1910, Rev. Suisse Zool., **18**: 68, worker. Type locality: Gembrook, Victoria. Syntypes: Mus. Hist. Nat., Geneva. New synonymy.

*Notoncus foreli* var. *subdentata* Forel, 1910, *ibid.*, p. 68, worker. Type locality: Forset Reefs, New South Wales. Syntypes: Mus. Hist. Nat., Geneva. New synonymy.

*Notoncus foreli* var. *acuminata* Viehmeyer, 1925, Ent. Mitt., **14**: 37, worker. Type locality: none cited; by inference eastern New South Wales. Syntypes: probably in Anthrop. Zool. Mus. Dresden. New synonymy.

*Notoncus rodwayi* Donisthorpe, 1941, Ann. Mag. Nat. Hist. (11), **8**: 206, female. Type locality: Nowra, New South Wales. Holotype: Brit. Mus. (Nat. Hist.). New Synonymy.

The worker of this species is variable in size, color, sculpture, angularity of propodeum, etc., and shows a wide range in the form of the upwardly projecting scutellum (see key to workers). However, the scutellum never approaches the tumuliform or ovoid shapes seen in the scutellar outgrowths of the related *N. gilberti* and *N. enormis*. The alitrunk and head are usually extensively and irregularly striate in varying directions, and the color ranges from light red-brown to piceous. Variation in most of the obvious characters appears to be partly size-linked (allometric), and partly independent of size. The largest and darkest forms seen, speaking in terms of averages, are those from the dry inland areas such as Wilpena Pound and Mildura. These more or less isolated (oasic) populations also show strong sculpture and tend to have the most strongly bifurcate or bicornuate scutellar apices. Series from the wet Dandenong Ranges, near Melbourne, are also dark, and are only slightly less heavily sculptured, but there is extensive local and intranidal variation in sculpture and in the depth of emargination of the scutellar apex. Populations from the dry, warm savannah woodland of southeastern Queensland tend to be smaller, smoother, lighter in color, and more often have the scutellum reduced to a chisel-pointed, or even a slender, acutely pointed process, though here again individual variation is very great. Population samples from intermediate areas and from the environs of Adelaide show all combinations of intergradient conditions connecting the forms described, and, except for the size-linked tendencies, geographical variation of independent characters seems to be highly discordant. Most of the various character-combinations seem to be very local, and all clinal trends are expressed crudely, at best.

The synonymy of this species has already been discussed in the summary of species-level taxonomy within the genus (above). An intensive study of the geographical variation in this species should prove to be most interesting; in many places it is a dominant ant, while in other places appearing suitable to the human eye, it is totally absent. The samples available may represent each a well-marked deme, but collecting has not yet been extensive enough to indicate the amount of discontinuity affecting the range of the species.

Localities for material studied: QUEENSLAND: Bundaberg (A. M. Lea). Brisbane (H. Hacker; B. Blumberg). Enoggera (W. M. Wheeler). Montville and ridge above Obi-obi River, Blackall Range, 300-500 m., pasture and lawn cleared from rainforest (W. L. Brown). Moggill, savannah woodland (Brown). NEW SOUTH WALES: Uralla; Salisbury Court (Wheeler). Albury (F. E. Wilson). Coff's Harbour, dry sclerophyll forest (Brown). VICTORIA: Ferntree Gully (F. P. Spry; Brown). Mt. Dandenong, 2000 feet, and One Tree Hill, Dandenong Ranges, grassy-floored moist sclerophyll forest, abundant (Wheeler; Brown). Vermont; Burwood, intermediate lowland sclerophyll forest (Brown). Mildura (F. H. Taylor). SOUTH AUSTRALIA: "Adelaide" (W. Pennifold). Wilpena Pound, Northern Flinders Ranges, dry *Callitris*-red gum savannah woodland, abundant (Brown).

### Nuptial Flight

A nuptial flight of this species was witnessed along the summit ridge of the Blackall Range, in and near Montville, Queensland, on May 21, 1951, beginning at about 11 A.M. on a fine, warm, sunny day. Earlier on the same morning heavy rains lasting through the previous week had ended, leaving the ground thoroughly saturated. In a cropped lawn at Montville, numerous small holes appeared, each opened by workers and accompanied by a minute pile of dark earthen particles. From these holes, males began to issue almost immediately in numbers, until within a few minutes there had accumulated on the surface a surprisingly large number of this sex and also a few workers. The males travelled aimlessly over the sward in low, flitting flight from one blade of grass to another, never rising more than a foot or so from the ground. Movement seemed to take place at random in

all directions. Suddenly, however, the males of one area all rushed simultaneously to a single focal point, which proved to be a winged female emerging from a small hole. In a few seconds, the female was surrounded by a dense swarm of males in the form of a ball, which at times must have exceeded 2 cm. in diameter. This ball moved in a half-tumbling, half-dragging motion over and among the densely packed grass blades, and held together for perhaps 20 seconds, after which the female escaped, flying straight upward. She appeared not to be encumbered by a male, and no males were seen to follow her for more than a foot above the ground; she flew steadily, and soon passed out of sight.

Meanwhile, the lawn had become dotted with similar balls of frenzied males, each surrounding a female in a fashion similar to the first. Obviously, many more males than females were involved in this particular flight. On each occasion, the female left the ball after 20-30 seconds and flew straight upward. I was not able to see whether all were unaccompanied by males, but none of those I saw up close had consorts in its flight after the first foot or so of the ascent. It is impossible to say, from these observations, whether mating takes place in the ball-formation on the ground, but this is my general impression, based on the lack of inclination in the observed males to fly at any distance above the ground.

During about 10 minutes, after which time the flight had begun to decline from peak activity, the males continued to search low over the grass, participating in each ball-formation encountered. About a half hour after the first appearance of the females, only males were to be seen flitting here and there or resting on grass blades. A few were seen visiting low flowering shrubs on a nearby fence row. At that time, I had to leave the scene, and the flight appeared to be at an end, with no more females appearing and the males rapidly disappearing by what appeared to be simple horizontal dispersal. No descending or dealate females were seen at this site at this time or later.

At 1 P.M. on the same day, on a part of the ridge about two airline miles distant, stray winged females of this species landed on my clothing while I was walking along a trail in sloping pasture. Others were found dealate, running over grass and bare spaces. No males were seen. At this place, a single dealate female of *N. enormis*, also apparently fresh from nuptial flight, was

found running over the open turf with the *ectatommoides*, though no nests of *enormis* were found by me in the Blackall Range.

The flight of *ectatommoides* was clearly an extensive and coordinated one over all or most of the ridge on that particular day, and was remarkable for the numbers of individuals produced. Previous collecting had indicated a rather modest population of the species, mostly nesting under stones, but the emerging males and females outlined instead, at least in one limited area within my range of view, a virtual continuum of underground galleries throughout lawn and pasture. A similar phenomenon occurs in the case of the flights of *Acanthomyops* species in North America and *Acropyga* in the Orient, both of which groups are subterranean in habits, and hence seldom suspected to be present in any numbers outside the flight season.

### Notoncus enormis Szabó

*Notoncus ectatommoides* Emery, 1895, Ann. Soc. Ent. Belg., **39**: 353, fig. 4, worker, *nec* female, *nec* Forel. Kamerunga, Queensland.

*Notoncus enormis* Szabó, 1910, Ann. Mus. Nat. Hungar., **8**: 368, fig. 6, worker. Type locality: Mt. Victoria, New South Wales. Holotype: Hungarian National Museum, Budapest.

*Notoncus capitatus* Forel, 1915, Ark. f. Zool., **9** (16): 90, pl. 1, fig. 8, worker. Type locality: Tamborine Mt., Queensland. New synonymy.

*Notoncus mjöbergi* Forel, 1915, *ibid.*, p. 91, worker. Type locality: Colosseum, Queensland. The types of this and the preceding species are probably in the Naturhistoriska Riksmuseet, Stockholm, and in the Forel Collection in the Geneva Museum. New synonymy.

*Notoncus capitatus* var. *minor* Viehmeyer, 1925, Ent. Mitt., **14**: 139, worker. Type locality: none cited; by inference, eastern New South Wales. New synonymy.

*N. enormis* is the most polymorphic among the *Notoncus* species as presently known. In the largest workers, the head is proportionately broader than in the smaller ones, and is more reddish in tone. The female is large and bulky, larger than in any of the other forms except the very large *spinisquamis*. Both worker and female are readily distinguished by the opaque sculpture and particularly by the well developed reclinate pubescence of the body in general, including the gastric dorsum. The worker scutellum, like that of *gilberti*, is rounded and projecting, but it varies more in size from series to series. A series from Bribie

Island, Queensland, follows Forel's description of *mjöbergi* in having a small, low scutellum, but this appears to be nothing more than an extreme in the normal variation of *enormis*. The synonymy has been discussed briefly under the heading of species-level taxonomy in the genus (above).

*N. enormis* is locally abundant in rainforest and subtropical wet sclerophyll forests, or their borders, clearings or successional stages, through eastern New South Wales and Queensland, north at least as far as the Cairns district of northern Queensland.

Localities for material studied: QUEENSLAND: Tamborine Mt., rainforest, second-growth forest of *Eucalyptus gigas*, and bordering cleared pasture land (A. M. Lea; W. L. Brown). Near Kondalilla Falls, Blackall Range, female just after nuptial flight, May 21, 1951 (Brown). Kuranda (Brown). Bribie Island (H. Hacker). NEW SOUTH WALES: Moree (A. M. Lea). "Near Sydney" (without collector). Katoomba (W. M. Wheeler). Bulli (F. H. Taylor). Dorrigo (W. Heron).

### Notoncus gilberti Forel

*Notoncus Gilberti* Forel, 1895, Ann. Soc. Ent. Belg., 39: 418, worker, female. Type locality: Mackay, Queensland. Syntypes: Mus. Hist. Nat., Geneva.

*Notoncus Gilberti* var. *gracilior* Forel, 1907, in Michaelsen and Hartmeyer, Fauna Südwest-Austral., Jena, 1: 299, female. Type locality: Fremantle, Western Australia. Holotype: Mus. Hist. Nat., Geneva? New synonymy.

*Notoncus politus* Viehmeyer, 1925, Ent. Mitt., 14: 39, worker. Type locality: Liverpool, New South Wales. Syntypes: Anthrop. Zool. Mus. Dresden? New synonymy.

*Notoncus gilberti* subsp. *gracilior* Wheeler, 1934, Jour. Roy. Soc. W. Australia, 20: 153, worker, female.

*Notoncus gilberti* subsp. *annectens* Wheeler, 1934, *ibid.*, p. 154, worker. Type locality: Enoggera, Queensland (by present selection); additional original locality, Brisbane, Queensland. Syntypes: Mus. Comp. Zool., Harvard. New synonymy.

*Notoncus gilberti annectens* var. *manni* Wheeler, 1934, *idem*, p. 155, worker. Type locality: Como, near Sydney, New South Wales (by present selection); additional original locality, Hornsby, New South Wales. New synonymy.

The worker of this species is very similar in the form of the alitrunk to *N. enormis*, but the sculpture is reduced to at most a very fine, loose, superficial reticulation, so that to all intents the

integument can be called smooth and shining, or even "polished." The mandibles, however, are finely striate over the usual scattered punctures, and the striation covers nearly the whole of their exposed dorsal surfaces; the clypeus is more or less distinctly longitudinally striate. The head in both castes, especially the female, is distinctly rectangular in full-face outline, with nearly straight sides, sharply rounded occipital corners, and a transverse, only feebly convex posterior occipital border.

Wheeler's 1934 subdivision of *gilberti* calls attention to the geographical variation, involving an apparent east-west size difference, plus other distinctions of size, color, sculpture, etc. supposed to mark different populations. However, the differences cited by Wheeler seem to be somewhat overdrawn; the smaller size of the western population is an average, not an absolute difference, and the samples from both east and west are still far from sufficiently representative for the purpose of testing significance of such variation. Even Wheeler recognized that some of the eastern samples were intergradient (subsp. *annectens!*), and then he never took into account Viehmeyer's obvious synonym, *N. politus.*

New material includes the piceous-colored examples from the hills around Canberra, and the isolated population sample from the Northern Flinders Ranges. These series add new dimensions to problems of geographical variation in the species, and at the same time show how inadequate our previous information was, and probably still is. For the time being, I prefer to emphasize the obvious kinship of all of the known samples by including them in the single species *gilberti,* without further distinction. Any future subdivision will have to take into account the realities of reproductive isolation between the various populations before it is formally made.

Localities for material studied: QUEENSLAND AND NEW SOUTH WALES: Type series of forms described by Wheeler; see synonymy, above. AUSTRALIAN CAPITAL TERRITORY: Kowen Forest, under rocks in open upland sclerophyll woodland, dark piceous variant (T. Greaves and W. L. Brown). SOUTH AUSTRALIA: Wilpena Pound, N. Flinders Ranges, under stone in entrance gorge, heavy riparian woodland of large *Eucalyptus camaldulensis* (Brown). WESTERN AUSTRALIA: Rottnest I.; Geraldton; Cottlesloe; Monger's Lake, near Perth

(W. M. Wheeler). King's Park, Perth (Wheeler; P. J. Darlington). Esperance; Norseman (E. O. Wilson). Wheeler took winged and newly dealate females near Perth on October 17 and 19, 1931.

### NOTONCUS HICKMANI Clark

*Notoncus hickmani* Clark, 1930, Proc. Roy. Soc. Victoria (n.s.) **42**: 126, fig. 1, no. 14, worker, female. Type locality: Trevallyn, Tasmania. Syntypes: Nat. Mus. Victoria, Melbourne.

*Notoncus rotundiceps* Clark, 1930, Proc. Roy. Soc. Victoria (n.s.) **42**: 127, fig. 1, no. 15, worker. Type locality: Albany, Western Australia. Syntypes: Nat. Mus. Victoria, Melbourne. New synonymy.

This species is smaller, more hairy (especially the underside of the head), and has proportionately shorter appendages than *N. spinisquamis,* and the gaster is oftener dark in color — in many series it is piceous. Size is very variable, both within and between nests of this species, and there exist partly allometric differences in head shape, alitruncal form, distinctness of ocelli, and completeness of striate sculpture; these differences appear to have been Clark's basis for separating the species *rotundiceps* from the original *hickmani.* Series at present available seem to indicate that Victorian-Tasmanian series from the higher-rainfall districts are larger on the average than those from New South Wales, the Victorian Mallee, South Australia and southwestern Australia; round-headedness and effacement of sculpture is in general correlated directly with the smaller size classes, but coloration is poorly correlated geographically with these qualities. Series from drier localities often seem lighter in color, regardless of size and sculpture.

*N. hickmani* occupies drier sites than does *N. spinisquamis;* in the Melbourne district, I found *hickmani* in open sclerophyll forest to the east of the city, and on the savannah to the north, in both places nesting at the bases of eucalypt trees. On the savannah at Broadmeadows, ants of this species were found on a cool, wet winter day resting in small groups beneath chips and bark lying on the ground at some distance from the nest. The ants forage at night on trees and shrubs.

Localities for material studied: In addition to syntypes of *hickmani* and *rotundiceps,* series from the following — NEW

SOUTH WALES: Dorrigo (W. Heron). VICTORIA: Sea Lake (J. C. Goudie). Burwood; Broadmeadows (W. L. Brown). SOUTH AUSTRALIA: Adelaide, dealate female in spider web, 16/V/04 (A. Zietz). Mt. Lofty (J. O. Tepper). Lucindale (Feuerheerdt). Encounter Bay (collector?). Sandy Creek (J. O. Tepper) and Ravine des Casoars (Brown), both on Kangaroo I. WESTERN AUSTRALIA: King's Park, Perth (W. M. Wheeler).

### NOTONCUS SPINISQUAMIS (André) new combination

*Melophorus spinisquamis* André, 1896, Rev. Ent., Caen, p. 254, worker, female, male. Type locality: Victorian Alps. Syntypes: Mus. Hist. Nat., Paris.

*Diodontolepis spinisquamis*, Wheeler, 1920, Psyche, **27**: 53. Clark, 1934, Mem. Nat. Mus. Victoria, Melbourne, **8**: 64. Wheeler, 1935, Psyche, **42**: 71.

*Melophorus* (*Melophorus*) *spinisquamis*, Emery, 1925, Genera Insect., **183**: 12.

This large, usually yellow or testaceous ant has very long legs and antennae, and the alitrunk is generally longer and more slender proportionately than in any of the other *Notoncus* species. In these same characters, *N. spinisquamis* also resembles *Aphaenogaster longiceps* (F. Smith), a common ant of the subfamily Myrmicinae with similar nocturnal habits and occupying the same localities.

The nest is usually or always built in the soil of moist or wet sclerophyll forest. Two nests I found in Sherbrooke Forest, Victoria, were under thick moss at the base of large *Eucalyptus regnans* trees, in a very wet, dark part of the forest. In each, only a handful of larvae and workers was found in what were probably only superficial chambers. I have seen other material from: VICTORIA: Millgrove; Beaconsfield; Belgrave (F. E. Wilson). Emerald (E. Jarvis). TASMANIA: King Island; Devonport (A. M. Lea). Isolated females from Victoria bear July and August dates.

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